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4.—Patterns of Life on Rocky Shores

Presidential Address, 1959

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I must at the outset explain my choice of title. At first sight this may appear more suitable for a popular lecture than for the Presidential Address to a scientific society. It is nevertheless carefully phrased to explain what I want to speak about. In the literature on littoral biology the term constantly used is 'zonation'. The paper most commonly referred to is one by T. A. and Anne Stephenson (1949) entitled, "The universal features of zonation between tide-marks on rocky shores", and many papers have been published describing the zonation of animal and plant life on rocky shores all over the world.

I have made such studies myself and am hardly likely to be accused of not appreciating their value if I appear critical in this attempt to examine the basis of such studies. I think the descriptive material supplied by these papers is of very great value and the attempt, expressed by the Stephenson's title, to discover universal features is an essentially scientific approach in that it attempts to relate observed facts in an orderly manner. However it seems to me that the study of zonation and the attempt to fit all littoral life into a universal pattern has become an end in itself, instead of a means to understanding the biology of the organisms which collectively produce this zonation and of the causal factors responsible.

Any study of the life of rocky shores reveals not only patterns of zonation in relation to sea level but other patterns which are just as important to an understanding of causal factors, and some of these may prove more accessible to experimental analysis. Moreover, study of patterns of life on rocky shores can give valuable information of general biological application. The littoral environment is a microcosm and as such is particularly suited to study if the right questions are asked.

In a presidential address one may be permitted to speculate in a way which might be out

of place in a rigorous scientific paper; this I propose to do.

Zonation

The fact that the animal and plant life of rocky shores displays a vertical zonation is at once obvious to anyone visiting a sloping rocky shore; it is less evident but just as real on the characteristic stepped limestone shores of south western Australia.

Two examples will serve to illustrate the type of distribution which has been described in most parts of the world.

1. Cape Leeuwin (lat. 34°S) at the southwesternmost point of Western Australia has sloping granite-gneiss rocks with moderate exposure to wave action at the point surveyed. The vertical distribution of the principal organisms found here is shown in Fig. 1. Below mean low water the rock is encrusted with coralline algae, lithothamnion, and there is a thick cover of brown algae. Above low water mark the dominant organisms are successively a limpet (*Patellanax*), a barnacle, another limpet (*Notoacmea*), a periwinkle, and a black film of blue-green algae. Among these a number of other organisms are common, each at its preferred level. The height to which the barnacle zone, and those above it, extends varies greatly with the aspect of the rock face.

2. Poste Lafayette on the east coast of Mauritius (lat. 20°S) has sloping basalt rocks and is exposed to strong, almost continuous wave action. The middle part (1 to 6 feet) above low water has many small regular depressions in which sea urchins live (*Echinometra* and *Stomopneustes*). From Fig. 2 it will be seen that again there is a fairly sharp upper limit to the larger algae in bulk, though individual plants occur higher. Above this there is a broad zone where three sea urchins (*Echinometra*, *Colobocentrotus*, and *Stomopneustes*) are the principal organisms, although three species of limpet are also common and a number of other organisms are present in smaller numbers, including barnacles. A narrow band with very

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few animals and a sparse growth of small algae is succeeded above by a film of blue-green algae on which periwinkles browse. It may be noted that one limpet, *Patella chitonoides*, is strictly confined to the lower part of the sea urchin zone.

Both shores display a characteristic zonation. The organisms which are thus zoned are the algae, sedentary animals such as limpets, and some rather more active animals such as the periwinkles. There are also common shore animals, grapsoid crabs and certain small fish which are much more active and move up and down with the water. With the exception of the last group all the animals and plants have their own specific levels where they are most abundant, thus forming a horizontal band along the shore. Often the numbers tail off gradually above and below, but in many cases their upper or lower limit is quite sharply demarcated. Sometimes a number of organisms share a common upper or lower limit; it is not just that individual species have their preferred levels on

valuable review paper, by Doty (1957), only became available to me after delivery of this address.

It is now generally agreed that shore zonation is "not a product of mere association or gregariousness, but that it is related to the differing tolerance by the organisms of the environmental factors that vary from high-water mark to low water" (Southward 1958). It is implicit in Stephenson's scheme of universal zonation that this is so. There can be little doubt that these variables acting directly or indirectly on the plants and animals do ultimately cause the observed zonation.

Many recent studies of life on rocky shores have concentrated on typifying the zonations of geographic regions, and authors have tried to relate the observed zonation to Stephenson's universal scheme. This is undoubtedly a useful descriptive device, because it facilitates comparison between shores in many parts of the world, and there is no doubt that the broad features

TABLE I

A scheme for describing the zones of plant and animal life on rocky coasts (from Southward 1958)

.....Extreme limit of spray or salt air.....		
Maritime land-lichens and salt-tolerant phanerogams		SUPRALITTORAL ZONE
.....Extreme limit washed by tides or waves.....		} SUPRALITTORAL FRINGE
Marine lichens and certain littorinids	SUPRALITTORAL FRINGE	
.....Level not washed by all tides.....		} INTERTIDAL ZONE OR LITTORAL ZONE
Barnacles, limpets, green algae, smaller brown algae and some red algae	MIDLITTORAL ZONE	
.....Level not exposed by all tides.....		} INFRALITTORAL FRINGE
Large brown algae, many red algae and calcareous algae: sometimes marine phanerogams	INFRALITTORAL FRINGE	
.....Extreme level uncovered by tides.....		} INFRALITTORAL ZONE
Some large brown algae, red algae and marine phanerogams		
.....Level at which there is not enough light for photosynthesis of algae.....		

the shore, but a number of animals and plants seem to share a common preference for a particular level.

This zonation has common features shared by shores all over the world. Littorinid molluscs colonise the upper rocks where they often get only spray or splash. Immediately below them, washed by the waves at every tide, there are usually dense colonies of barnacles. A more varied assortment of animals and plants commonly takes over lower down, and at about mean low water certain large algae (*Laminaria* and *Ecklonia*) become dominant; this last change is particularly well defined on our granite shores.

The fact that these broad zones can be recognised on rocky shores almost anywhere throughout the world has led T. A. and A. Stephenson (1949) to propose their 'universal' scheme of zonation. This scheme has been very generally adopted by writers on intertidal biology, though there has been disagreement about the exact limits of the zones and the names applied to them. The scheme is summarised in the accompanying table from Southward (1958) who has recently reviewed the whole subject of zonation on rocky shores. Another

of the zonation can be recognized in most places. There are however certain dangers attendant on this approach, and these I want to examine briefly.

Perhaps the most serious danger is that description of the zonation can easily become an end in itself and so discourage further study. The synecological approach will be particularly unprofitable if it does not point the way to an understanding of the causes of zonation. Causes are considered by Southward (1958) and formed the principal subject of an interesting discussion by Stephenson (1943) and others at a symposium of the Linnean Society of London. However much detailed work on individual species will be needed before there can be a full understanding of the complex patterns on most shores.

A second danger is that by fitting observed patterns into a general scheme real differences may be obscured; differences which may in themselves be very informative. The difference between the zonation of wave beaten and sheltered shores has received considerable attention, and the information derived from such comparisons has proved valuable. There

are however other physical variables which influence the distribution of shore animals. These include: the mechanical action of the waves, the pounding and tearing action of which inhibits some organisms and favours others; the angle of slope of the shore; the nature of the substrate, whether hard or soft, porous or relatively impermeable to both water and filamentous algae; the presence of crevices in the rock. Perhaps these are only 'modifying factors' for zonation, but all are a significant part of the environment, and as such may be the immediate factors which favour one species rather than another.

More subtle however is the danger that just because the zonation can usefully be described by a universal nomenclature, the vertical movement of the water line on which this system is based may be thought to produce its effect in a uniform manner. On the one hand movement of the water line is itself complex, varying both in range and periodicity and it would be surprising if the results it produced on the shore environment were uniform. I will return to this later. On the other hand the many species which collectively produce the zonation respond in different ways to the physical components of the varying weather of the shore: temperature, insolation, and moisture.

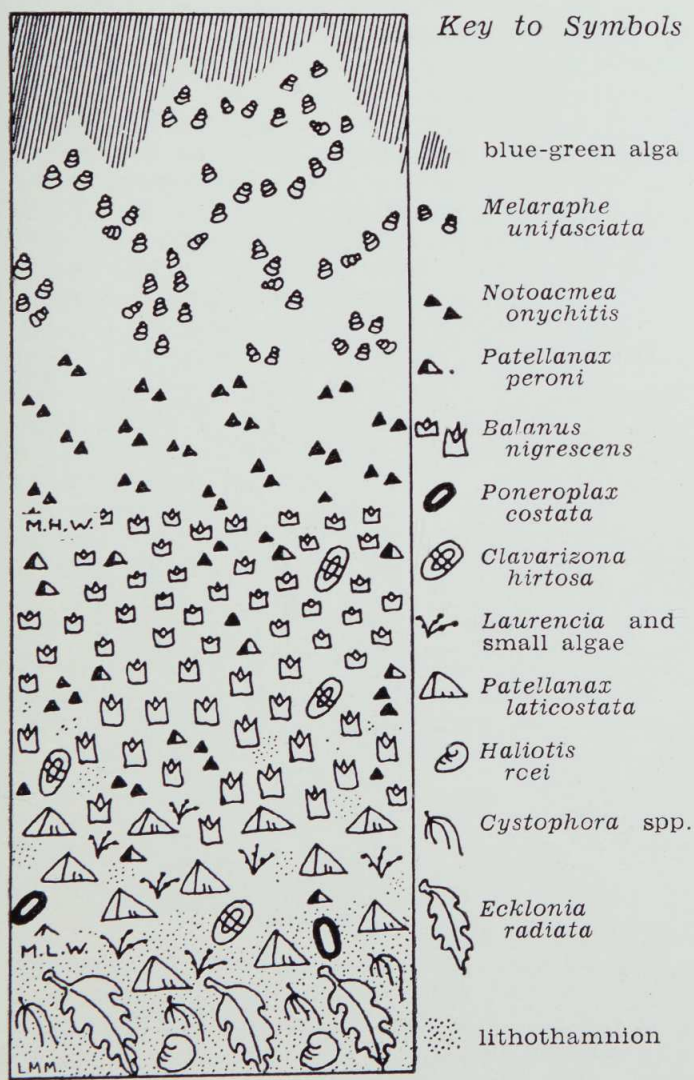


Fig. 1.—Cape Leeuwin, Western Australia. The littoral fauna and flora of a sloping rock surface with moderate exposure to wave action.

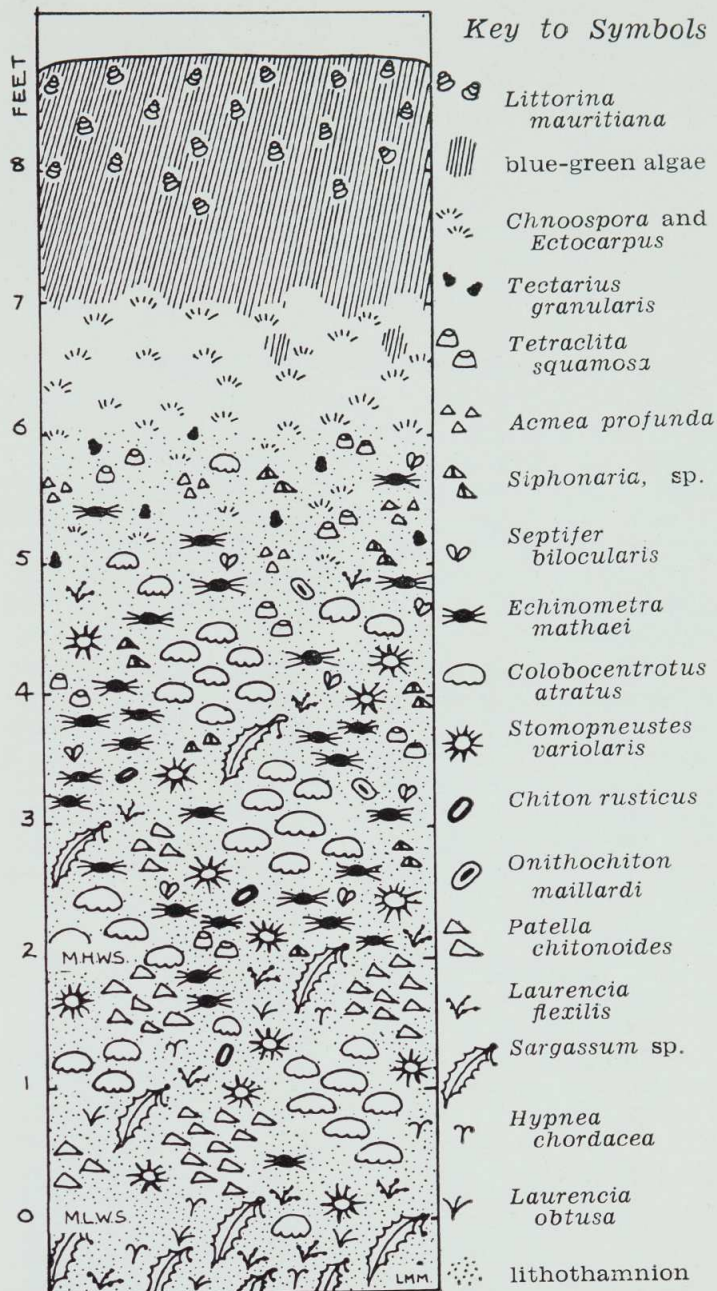


Fig. 2.—Poste Lafayette, Mauritius. The littoral fauna and flora of a sloping rock surface exposed to constant wave action.

A fourth danger in the zonal approach is that it is static. The very uniformity recognised in the zonation implies a permanence. But the individual organisms, and the groupings of these, which collectively make up the zones are transient and study of their dynamic interactions is more likely to be informative than observation of apparently static distributions.

This has been brought home to me forcibly recently. Exceptionally low tides and calm seas in January of this year destroyed the entire animal life of certain reef platforms on our west coast (Hodgkin 1959). It is too early yet to know whether these species will re-establish themselves, but other species of animals and plants have already replaced them in the space left vacant after the catastrophe.

This is a particularly striking example of sudden change in distribution, but there are many features of the patterns of shore life which cannot be adequately explained in terms

of the physical attributes of environment alone and require an understanding of the interrelations of the animals and plants themselves.

I propose first to consider briefly the water movements which cause the characteristic fluctuation in physical environment—the weather of the shore—and then to discuss some of the immediate factors which determine the patterns of life on rocky shores, more especially interrelations of organisms.

Water Movements and Zonation

It is, I think, unfortunate that the zonation is so often called 'intertidal', or 'zonation between tide-marks' to use Stephenson's phraseology. The term 'tide' and its derivatives have precise meanings; the shore zonation normally extends well beyond the limits of the tides, the supra-littoral fringe is a product of wind and waves, and the use of these terms is therefore inaccurate.

They are also misleading because they place an undue emphasis on the tidal factor in zonation. Stephenson and Stephenson (1949) state that: 'The primary cause of it [zonation] is the existence of an interface between air and water'. But, as stressed by Southward (1958), it is 'rise and fall of the water line produced by the tides or waves, or both [which] must be regarded as the primary cause of the observed patterns of zonation'.

The emphasis on tides as the ultimate cause of zonation probably derives from the fact that most studies have been made on shores with a considerable tidal range. The zonation in such places is a 'tidal zonation', though modified by the degree of wave action. In the Mediterranean, which is almost tideless, or in the growth on a ship's hull the plants and animals are also clearly zoned. The exposed Mauritius shore described above is a good example of 'wave-zonation'—one caused mainly by continuous wave action. Here the mid-littoral zone has three times the vertical range of the tides. The sheltered shores of Mauritius have a totally different fauna and flora, and the littoral has a vertical range which corresponds to the small tidal range. Again this is a 'tidal zonation'.

The 'climate' of these two types of shore will obviously be very different. The difference is particularly striking in tropics and subtropics where the shore is subject to intense heating during the day. In the absence of continuous wave action, tropical shores have a short turf of small algae or are dominated by animals; there is not the heavy cover of large brown algae so common on temperate shores. The importance of this 'latitudinal effect' may be noted here in passing.

The immediate physical factors which constitute the climate of the shore (temperature, insolation, and wetting and drying) vary with position in the vertical range of movement of the water line. However, this movement of the water line is complex. The waves and tides which cause it vary independently both in vertical range and periodicity. Waves have periods of seconds and their amplitude varies irregularly. Tidal fluctuations have periods of 12 and

24 hours, 14 and 28 days and recur with great regularity. Diurnal and semi-diurnal tides are different in their influence on the relative duration of emergence and immersion and there are longer period seasonal and irregular fluctuations of level. Even the time of low tide has been shown to be important (Lawson 1957).

Before leaving the subject of zonation let me summarise the position as I see it. On any shore where there is water movement, however caused, the major zones which have been generally recognised certainly exist. However variability of the biological material, latitudinal effect, and the lack of uniformity of water movement, make it impossible to define precisely zone boundaries which will have universal application. To do so is to impose an exact classification where none is warranted, one which can obscure data that are important to an understanding of the relation of organisms to their environment.

Causes of Shore Patterns

Andrewartha and Birch in their book 'The Distribution and Abundance of Animals' divide the environment of an animal into four components: weather, food, other animals and organisms causing disease, a place in which to live. Their discussion relates mainly to terrestrial animals, but I hope to show that this analysis of environment is valuable also in the study of littoral populations. I am not suggesting that concepts derived from a study of terrestrial animals should be carried over to the littoral environment without careful examination and without due weight being given to the peculiarities of the situation. One such peculiarity is that littoral populations occupy a band which may be of great length, but is seldom more than a few yards in width. Another is that dispersal of immature stages is often largely passive.

Andrewartha and Birch stress the need to study the interaction between individual species and their environment; I do not question the wisdom of this approach, but I think that in some cases we may profitably consider the animals of small phyletic groups collectively and also sometimes the ecological replacements of particular animals. For example, both barnacles and limpets may be considered in this way. Several species of each occur at different levels or in particular habitats, while on other shores they may be replaced by quite different animals.

Of the four components of the environment, weather has received most attention in studies on littoral organisms (e.g. Broekhuysen 1940, and review in Southward 1958). The other components were, food, other animals and a place in which to live. I propose now to consider particular animals, or groups of animals, in respect of these three components of their environment more especially.

My purpose is to discuss what information is available and what can usefully be sought that will help us to understand the distribution and abundance of these animals. I am afraid I shall not be very systematic about it. It is seldom possible to fit the animals neatly into any particular pigeon hole and, as I said at the outset, I propose to be speculative.

Larval Settlement and a Place in which to Live

The eggs and early stages of many shore organisms are distributed by the sea water; they are planktonic and have to settle on or attach to the rocks before they can feed and grow. The initial settlement may be just as important in determining the ultimate distribution of the animals and plants as influences which operate on the adult organisms.

I will give two examples. 'Most European species of barnacles have been shown to be gregarious; the cypris settles and metamorphoses most easily in areas inhabited by adults of the same species or a closely related one, or on substrata bearing traces of a former adult population' (Southward 1958). Thus settlement is not random, although new surfaces are of course colonised. Barnacle populations tend to be self-perpetuating and dense stands result, in which few other animals live.

The limpet *Patelloida alticostata* occurs alone over considerable areas of the intertidal platforms on our coast. In November 1954 a party of Zoology students cleared every limpet from four square yards of a reef platform at Rottnest Island. Before clearing there were 400 to 500 limpets per square yard and no other animals or plants on the rock. Within a few days of their removal there was a dense growth of filamentous algae which was replaced by coralline algae over the next few weeks.

Five years after the original clearing the limpets have still not fully re-established themselves. Some have managed to invade the area from the edges and a few have settled within it, but there is a thick growth of weed and the limpet population is still less than half that outside where there is no weed. The change in environment brought about by the establishment of the weed prevented settlement of young limpets. The limpet population like the barnacles is normally self-perpetuating, it excludes macroscopic algae and other animals and so maintains its own place in which to live.

The clearing experiment was repeated on a vastly greater scale by the catastrophe of which I spoke earlier. The entire population of *P. alticostata* was destroyed on certain platforms at Rottnest (January 1959). During the succeeding twelve months two pulmonate limpets have invaded the virgin fields of small algae (there is no coralline mat). Unlike *Patelloida* these limpets lay non-planktonic eggs all the year round. It is too early yet to know what will be the final outcome.

Other examples of what appear to be self-perpetuating populations are seen with the large limpet *Patellanax laticostata* and the mutton fish *Haliotis roei*. These, with *P. alticostata*, two chitons and an anemone are the principal fauna of the outer edge of our intertidal limestone platforms. In some places all occur together, in others one is dominant to the almost total exclusion of the others, the rock is grazed bare of algal growth and takes a form characteristic of the species. In such places each *P. laticostata* has a smooth shallow channel of four or five times its own area and often continuous with those of its neighbours, and *Haliotis* occupies shallow depressions of about its own dimensions. So long as these forma-

tions persist they certainly favour the particular species just as the bare flat surface favours *P. alticostata*. These animals are not confined to such places, but they are much more abundant in them than elsewhere.

Two rather different examples of limitation by available places in which to live are afforded by another limpet and a sea urchin. *Patelloida nigrosulcata* lives principally on the shells of other gastropods, chiefly the large limpet *Patellanax laticostata* and the mutton fish *Haliotis roei*. Usually there is only one *nigrosulcata* to each shell, and each shell is grazed bare. Although not every shell has its *nigrosulcata*, most have. Unoccupied shells are usually covered by a thick growth of algae—again an impenetrable jungle to a young limpet trying to find a place to settle.

The tropical sea urchin, *Echinometra mathaei* is abundant in the littoral on the wave-beaten rocky shores, such as the Mauritius shore described earlier and on the exposed west end of Rottnest. In such places it is confined to characteristic burrows in the rock; each animal has its own 'home'. On the Mauritius shores almost every potential home in the mid-littoral is occupied by a sea urchin and the density of population appears limited by the number of available homes. On the more exposed east coast *Stomopneustes* competes with *Echinometra* for these homes, but on the west coast *Echinometra* has the field to itself. In December 1957 there were vacant homes above the upper limit of distribution of the urchins; perhaps they are occupied at other seasons, but at that time they were above the level of continuous splash.

Weather

Weather is of such obvious importance in determining the distribution of intertidal animals that it has received much attention from workers on shore organisms. I do not want therefore to say much here, but will give a few examples of how weather limits the vertical range of organisms.

Above the intertidal platforms of our W.A. limestone shores the rock is generally vertical or overhanging. Here four or five feet of the rock face, the upper mid-littoral, is generally dominated by two limpets—*Notoacmea onychitis* and *Siphonaria luzonica*. These limpets establish their own 'homes' to which they return at low tide, but they evidently move house periodically. Each winter some of the larger limpets get so high on the rocks that when summer comes, with its lower sea level, calmer seas, and higher temperatures, the more adventurous animals are killed by heating and desiccation. In winter the sporelings of a variety of algae also establish themselves on this rock face. They never survive the lower sea level and calmer seas of spring. *Patelloida alticostata* colonises the lower one foot of the rock, below *Notoacmea* and *Siphonaria*. I have never seen it dying here, but I suspect that its upper limit may be determined by the height to which a sufficiency of interstitial water is retained in the rock.

There is a similar seasonal mortality among juvenile barnacles on the granite rocks of our south-west. In early summer many empty

juvenile shells can be found on the rock above the main mass of *Balanus nigrescens*. The obvious assumption is that they have been unable to withstand heating and desiccation at the higher levels, however there is heavy predation by the whelk *Dicathais aegrota* and this is at least an important contributory cause of mortality.

Food

Andrewartha and Birch say that the number of animals in a population is seldom limited by shortage of food. The source of food of littoral animals is twofold: firstly the food which comes to them in suspension in the sea water and secondly the food which grows on the rocks. The amount of food available to suspension feeders certainly seems to affect their rate of growth, as indicated by the observations of Barnes and Powell (1950) but how far this is important in determining distribution in bulk is more difficult to decide. Barnacles, mussels, serpulids all commonly are packed tight, often entirely covering any surface on which they settle. The situation is very different for grazing animals. These feed actively, mainly on algae which grow on the rocks, and I suspect that for them food may often be a limiting factor.

Limpets furnish examples of natural populations which do 'consume a large proportion of the food available to them.' The populations of *Patelloida alticostata* of which I spoke earlier keep the algae on which they feed grazed down to bare rock, in fact they even remove rock particles in the process. Between 600 and 700 small to medium sized limpets per square yard seem to be the maximum population these resources can support. A population of this kind covers an area of platform at Green Island, Rottneest. But a small part of this same platform carries a population of no more than 200 large limpets per square yard, again to the exclusion of all other life. They are still fully utilising their food resources. Obviously food alone cannot here be limiting the actual numbers of animals, though it may limit the biomass which can be supported. The figures (Table II) suggest that recruitment to the population is greater in the first case than in the second and the subsequent history supports this. Perhaps I should have discussed this example under the heading 'Other animals of the same kind'. Here the natural situation approximates the experimental one in which the food is constantly replenished by the experimenter.

TABLE II

Numbers and Size distribution of *Patelloida alticostata* from ¼ sq. yard areas of rock

Greatest diameter cm	<i>P. alticostata</i> in experimental areas:							
	A1	A2	B1	B2	C1	C2	D1	D2
1.0 - 1.5	68	—	81	—	0	1	0	1
1.5 - 2.0	29	—	51	—	6	22	0	10
2.0 - 2.5	47	—	40	—	7	17	2	8
2.5 - 3.0	1	—	0	—	24	23	19	27
3.0 - 3.5	0	—	0	—	9	0	13	4
Total measured	145	—	172	—	46	68	34	50
Total removed	152	175	189	173	47	68	33	51

Regulation of animal numbers by other animals of the same kind would lead me to the dangerous ground of controversy over density dependent and density independent factors and this I do not propose to attempt to discuss.

Other Animals of Different Kinds

The two limpets *Notoacmea onychitis* and *Siphonaria luzonica* mentioned earlier under 'weather' share the same vertical zone either as a mixed population or with one or the other locally dominant, and they browse on the same sparse algal flora. Are they between them utilising the whole of the resources available to them? If they are, what ecological differences are there between them which enable them to live alongside one another instead of one replacing the other? I cannot suggest an answer here, but in analagous situation I can offer a partial answer.

There are two species of *Siphonaria* on Rottneest, *luzonica* and *baconi*. Sloping intertidal rock surfaces are the exception on W.A. limestone shores, but one such shore carries a mixed population of these two species. They are present side by side and appear to be utilising the same resources. However counts of the limpets show that *luzonica* predominates at the higher levels and *baconi* at the lower.

On the sloping rocks the two species live together in an environment that varies continuously. On the more usual stepped shores there is a separation of the two species; *luzonica* lives on the undercut face which is subject to drying at low water, *baconi* is seldom common but lives either at the foot of the undercut and onto the platform or submerged in small intertidal rock pools. In this case the area of overlap between the two species is small producing a zonation that is not evident on sloping rocks.

Where two species of animal utilise the same resources and the resources are limited, one animal may totally exclude the other, or they may both survive and share the resources. In the latter case they may intermingle freely or a patchy distribution of the two may result. (In laboratory experiments with insects these situations have all been achieved by suitable manipulation of the conditions).

I have already given an example of the first situation. *Patelloida alticostata* occupies considerable areas of platform from which all other animals are excluded. Given the right conditions *Haliotis roei* will cover the rock to the exclusion of every other animal; there is just such a population at Yanchep near the edge of the reef platform.

One might include the suspension feeders in this category too, because some of the barnacles, rock oysters, and serpulid worms occupy belts to the total exclusion of other macroscopic animals, but since the adults are completely sedentary the situation is very different. One might be justified in regarding them as plants, ecologically.

The second situation of two animals sharing the resources is illustrated by the two limpets *Notoacmea* and *S. luzonica* mentioned above, also by the urchins *Echinometra* and *Stomopneustes* on the east coast of Mauritius. The two species of *Siphonaria*, while sharing a

particular habitat have slightly different vertical ranges, as also have the two periwinkles *Melaraphe unifasciata* and *Tectarius rugosus* which inhabit the supralittoral fringe of our coastal rocks. It would be surprising if there were not also some difference in the requirements of the species mentioned first which are much less closely related to one another.

A careful analysis of the differing requirements of a large group of sympatric species of the predatory gastropod *Conus* is given by Kohn (1959).

The third situation, of a patchy distribution, may again be illustrated from Mauritius. Near low water level, on wave beaten shores, flat rock surfaces are colonised by a green alga. (*Chaetomorpha antennina*), a limpet (*Patella chitonoides*), and a sea urchin (*Colobocentrotus atratus*). In some situations their distribution is markedly patchy, one particular area of rock is covered with weed, another with limpets, and a third with urchins, in each case to the exclusion of all other macroscopic life.

I mentioned earlier a somewhat similar situation on some of our limestone platforms where patches of *Haliotis* sometimes alternate with *Patelloida alticostata*, each in its own place excluding all other animals. As stated there I think this is because the preferred microhabitats are not identical.

This explanation may apply also to the patchy distribution of limpet, sea urchin, and sea weed; their requirements may be slightly different, but although the areas involved are smaller, I think this case is more akin to that of the pure stands of *Patelloida alticostata* where the one animal utilises all the resources and excludes all other animals. I will return to this later.

I have spoken only of relatively simple situations in the interrelations of animals because these are most susceptible of analysis. However before leaving this subject I must mention briefly

TABLE III

Fauna of outer reef flat at different localities

Cape Vlaming is exposed to heavy wave action, Carnac West reef is less exposed, and Point Atwick is only moderately exposed

	Rottneet I. Cape Vlaming	Carnac I. West reef	Garden I. Point Atwick
Coelenterata			
<i>Isanemonia australis</i>	+	+	—
Amphineura			
<i>Poneroplax costata</i>	+	+	—
<i>Clavarizona hirtosa</i>	+	++	—
<i>Onithochiton occidentalis</i>	+++	++	+
Gastropoda			
<i>Haliotis roei</i>	—	+++	+++
<i>Patellanax laticostata</i>	+++	+	—
<i>Patelloida alticostata</i>	+	+++	++
Crustacea			
<i>Balanus nigrescens</i>	+++	—	—
Algae			
lithothamnion	++	+++	+
large algae	+	+	+++
Height of reef flat above M.L.W, feet	2.0	1.2	0.5

TABLE IV

Fauna of outer reef flat at Yanchep.

The outer edge of the reef flat is straight, and all parts are equally exposed to wave action.

Height of reef flat above M.L.W., feet	0	0.8	1.5	2.5	4.0
<i>Modiolus pulex</i>	—	—	—	—	++++
<i>Notoacmea onychitis</i>	—	—	+	++	+
<i>Patellanax peroni</i>	—	—	+	++	+
<i>Poneroplax costata</i>	—	—	+	++	++
<i>Balanus nigrescens</i>	—	—	+	+	+
<i>Clavarizona hirtosa</i>	—	+++	++	++	—
<i>Patelloida alticostata</i>	—	+++	+++	—	—
<i>Haliotis roei</i>	+	+++	++++	+	—
<i>Onithochiton occidentalis</i>	—	++	—	—	—
<i>Isanemonia australis</i>	—	+	+	—	—
<i>Patellanax laticostata</i>	+	—	—	—	—
lithothamnion	+	+++	+	—	—
blue-green algal film	—	—	+	++	—
large algae	++++	—	+	—	—

the more complex situation so often found on the shore where a number of species share a particular zone. This is well illustrated by what I call the 'outer edge fauna' of the Western Australian limestone reefs. Here, where the waves break hardest there is a mixed fauna usually with three or four macroscopic species really common and several other less common species. As shown by Tables III and IV the composition of the fauna varies from place to place, both with the degree of wave action and the level of the rock in the tidal range. Sometimes the mixed population is so dense that the rock is grazed bare. More often however coralline algae encrust the rock thickly, the same animals are scattered through this, and it provides macrohabitats which give refuge to a variety of smaller animal life.

Finally under this heading 'other animals of different kinds' I must mention predators. There is no dearth of predators in the littoral and there is plenty of evidence that whelks and cone shells, starfish and even gulls all take their toll. They may well be important in regulating the number of animals near the limits of their vertical range and thus help in maintenance of the zonation. I mentioned this in reference to *Balanus nigrescens* and *Dicathais aegrota* above. Barnes and Powell (1950) describe just such heavy predation on high level populations of barnacles on cleared rock surfaces on the Scottish coast. There is also no doubt that they attack these animals well within the preferred range, but what part they play in determining animal numbers and distribution is difficult to decide. Fischer-Piette (1935) describes how the whelk *Purpura lapillus* caused the relative abundance of barnacles and mussels in a mixed population to change. Initially barnacles were dominant, but heavy predation allowed mussels to replace them, the whelk then changed its feeding habits, the mussels were depleted and barnacles colonised the rocks again.

Dynamics of Shore Populations

This last example emphasises the dynamic character of shore populations. Both the shore zones and more localised groupings of animals and plants have a remarkable persistence, how-

ever they are certainly not static. A clear example of large scale change was given by the January catastrophe of which I spoke earlier. The same catastrophe resulted in the colonial anemone *Actineogeton* almost completely replacing all other life on one platform, only to be replaced in its turn by a mixed population more akin to that originally occupying the area. In another place the mussel *Septifer* replaced *Echinometra* for a time and there has been no sign yet of recolonisation by urchins. There have been other great changes and it will be instructive to see whether the original populations eventually re-establish themselves; whether in fact they represent relatively stable terminal communities (climaxes) or whether they are merely adventitious associations which may arise from time to time in this situation.

I gave earlier examples of seasonal changes in animal and plant populations on our limestone coast. I also mentioned the observation of Lawson (1957) that changes in the distribution of algae resulted from seasonal differences in time of lowest low water. These are of interest not only as evidence of constant change, but also because they indicate that these sort of changes may be important in producing the more persistent patterns.

But quite apart from catastrophes and seasonal fluctuations, shore populations are in dynamic rather than static equilibrium, and even though certain associations can be recognised as characteristic of particular levels the component parts are in constant flux. Shore animals and plants do not survive long individually, seldom more than a few years, they die or are destroyed by various agencies and are replaced by other organisms of the same or other kinds; there is constant competition for the available resources. Under these circumstances it is remarkable that shore communities do achieve a considerable measure of continuity. These communities are often so complex that any attempt at an analysis of the interrelations of the organisms is likely to be unprofitable. There are however simpler situations such as those discussed above where a knowledge of the biology of the few species present offers an opportunity to understand their interrelations.

One aspect of these situations bears amplification. I have described above examples of self-perpetuating populations covering considerable areas of rock. Patchy distributions may also be partly explained by the inability of interlopers to establish themselves. This is beautifully illustrated on some Mauritius shores where the urchin *Colobocentrotus* is found alone on certain rough limestone surfaces. In these urchin preserves of a few square yards in extent the only visible algae are those which cling to pinnacles of rock inaccessible to the urchins and the only other animals are a few daring interlopers belonging to more active species such as the turban shell *Turbo setosus*. Grazing pressure prevents macroscopic algae and young animals of other species from obtaining a foothold. T. A. and A. Stephenson (1949) illustrate the effect of brown algae in preventing settlement of barnacles.

Presumably in such cases the animal or plant has some slight ecological advantage over its neighbours. Such a situation, of two self-perpetuating populations each with slightly different ecological preferences must result in sharp boundaries between them. Again this is well illustrated from a Mauritius example. I found there that in passing from a more to a less wave-beaten situation *Colobocentrotus* was replaced by the limpet *Acmea profunda*, the two were mutually exclusive. In the more exposed part there was an equally sharp boundary in rising up from the band of *Colobocentrotus* to the *Acmea* above. Thus the vertical zonation showed a sharp boundary—a common feature of zonation.

Conclusion

I warned you I would speculate, and this I have done. I have put forward hypotheses to explain patterns of which I have spoken and I believe these are justified by the observations. To test them is quite another matter. However many of these problems are accessible to experiment in field or laboratory.

Much has been done with algae and also with some animals to find out how weather may determine their distribution on the shore, with valuable results. I do not doubt that weather is the principle component of the environment limiting the distribution of some animals. Clearly also shore climate ultimately determines the broad outlines of the zonation. I have tried however to show that observed patterns of distribution commonly result from more immediate factors: food and grazing pressure, available places in which to live, hazards of larval settlement, predation. These will be more difficult to study in the laboratory, particularly as they probably seldom act singly, but they should be accessible to analysis by relating laboratory and field experiment to observation in the field. But if this is to be done attention will have to be concentrated on individual species before the interrelations of complex associations can begin to be understood.

The littoral environment is certainly complex and there are considerable difficulties associated with study of its ecology. However I do not think it is any more complex or difficult of analysis than many terrestrial situations which ecologists have attacked with considerable success.

Acknowledgments

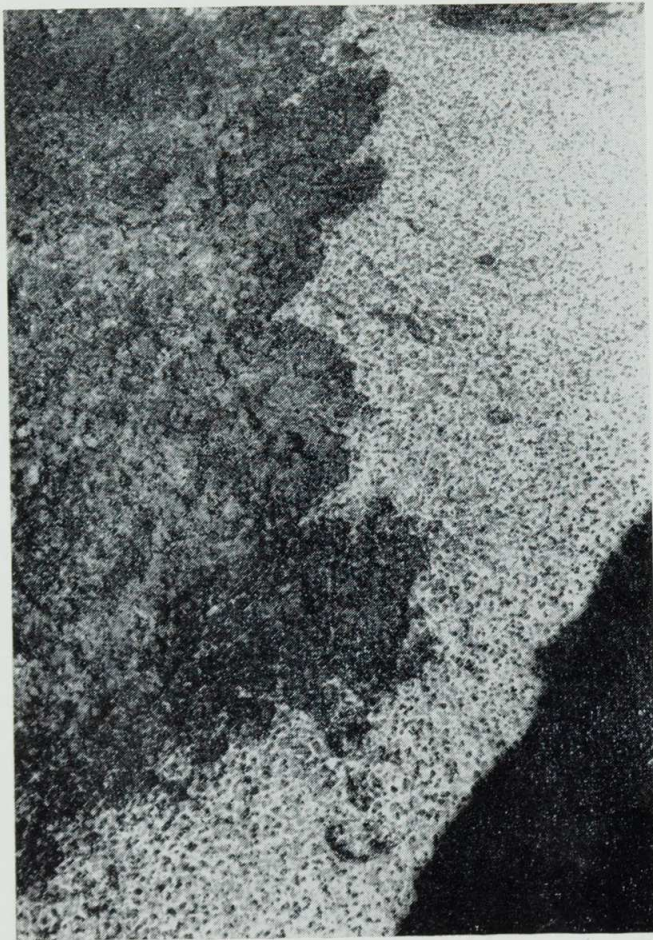
The investigations on which these observations are based were made with the help of a research grant from the University of Western Australia. I am indebted to many colleagues for the helpful discussions I have had with them on my theme and especially to Mrs. L. Marsh who has been associated with me in studies of the Western Australian littoral fauna.

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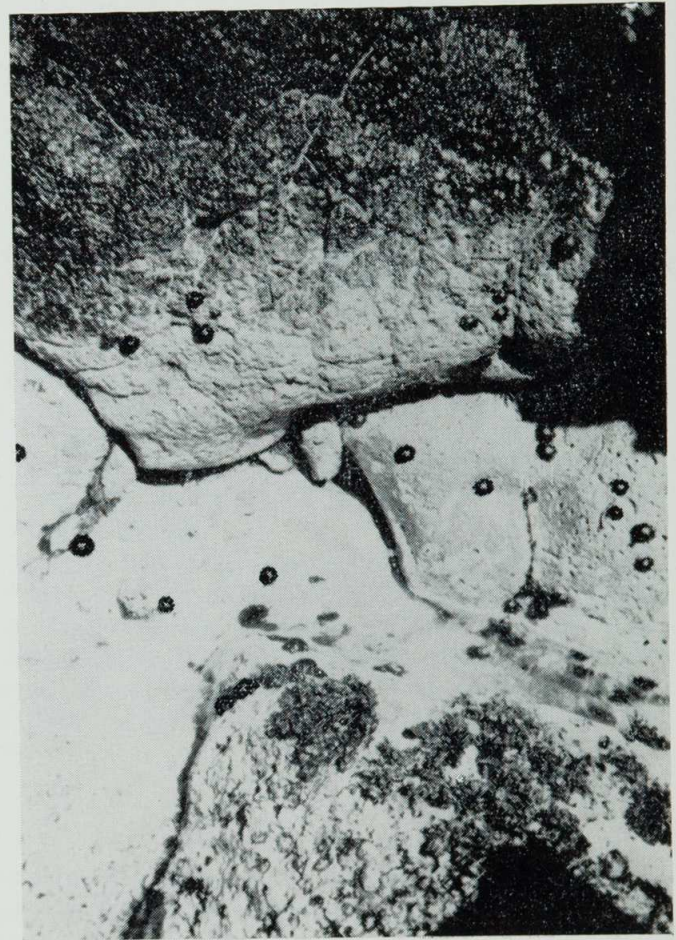
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1.—Intertidal limestone platform, Cape Vlaming, Rottnest Island. *Patelloida alticostata* dominant here before "catastrophe" of January 1959.

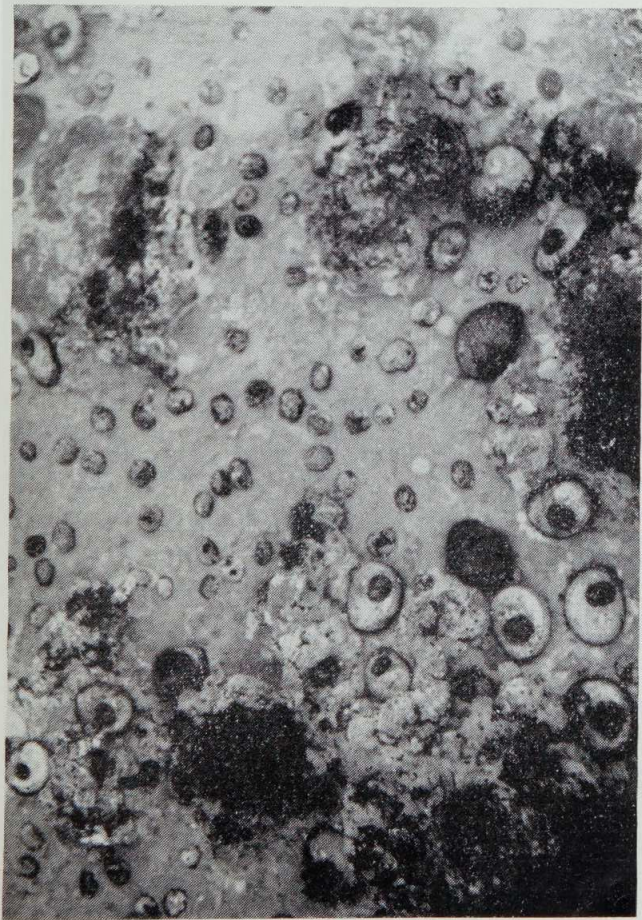


2.—Limestone platform with coralline algal association on left, *P. alticostata* alone on right (black at bottom right is shadow).

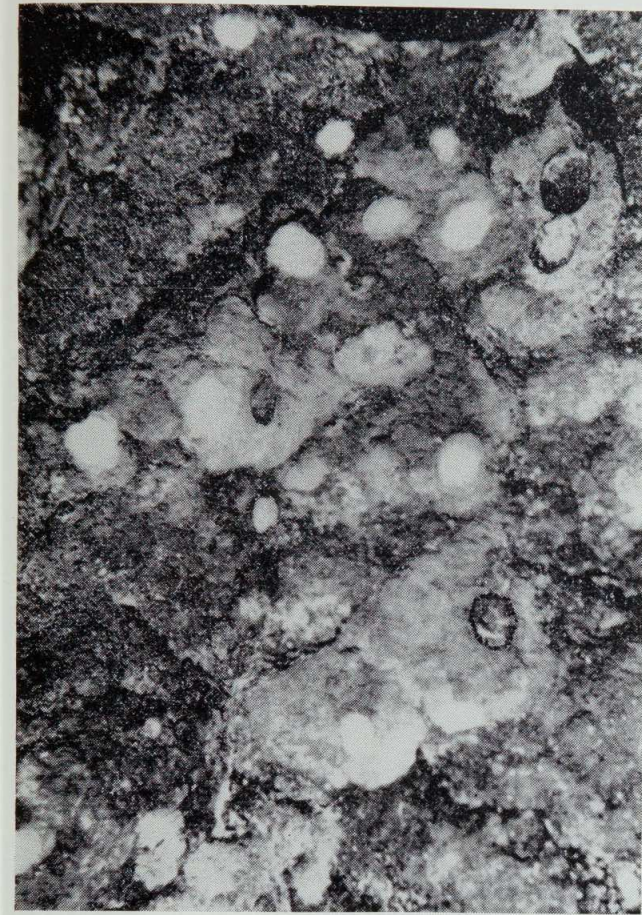


3.—Intertidal basalt rock (Mauritius) with *Colobocentrotus* on thin lithothamnion across centre; blue-green alga above.

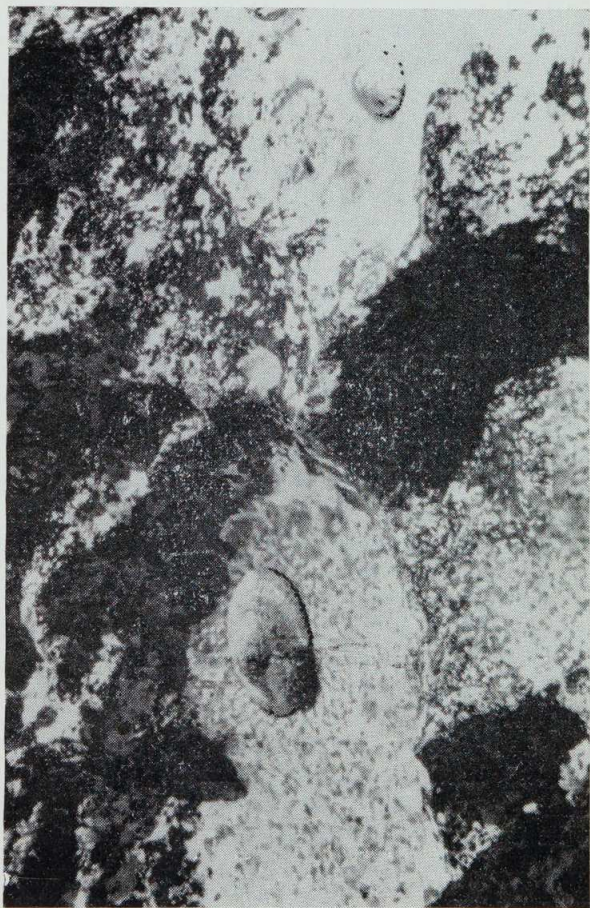
PLATE I



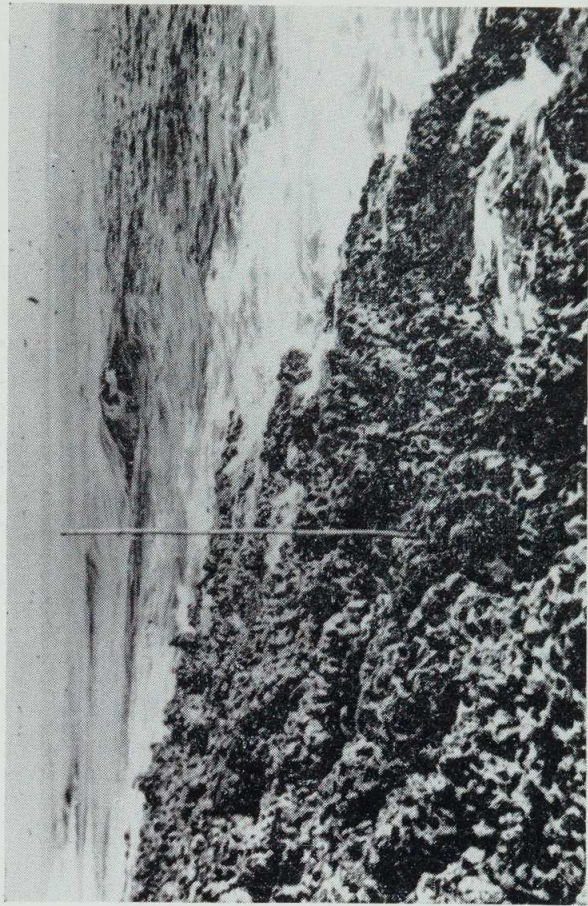
1.—*Haliotis roei*, *P. alticostata*, and encrusting lithothamnion on outer part of limestone platform. Note two *Haliotis* are weed-covered, but others are bare and each carries a *Patelloida nigrosulcata*.



2.—Empty limpet "homes" on limestone above high water in summer. One *Siphonaria luzonica* and three *Notoacmea onychitis* survive.



3.—*Patellanax laticostata* in typical "garden" on limestone. The limpet is bare of weed, but carries a single, weed-covered *P. nigrosulcata*. *P. alticostata* at right.



4.—Basalt rocks of exposed shore at Mauritius showing sea urchin burrows. (Six foot pole).

PLATE II